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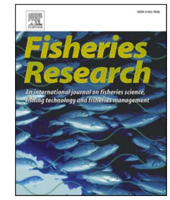

Review

Best practices for catch-and-release shark angling: current scientific understanding and future research

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ABSTRACT

In recent decades, the abundance of sharks in the world's oceans has decreased due to overexploitation by commercial fisheries. Over this same period, sharks have been increasingly targeted for sport by recreational anglers. "Catch-and-release" (C&R) angling, where sharks are released alive after capture, has been proposed, and in some situations, mandated as a conservation measure in recreational fisheries. In C&R fisheries, anglers are encouraged to follow best practices, each with the goal of maximising post-release survivorship (PRS) of angled fish. Here for sharks, we review C&R global best practices and the science underpinning them. Despite shark C&R fishing being practiced globally, peer-reviewed research into post-release survivorship is limited to just twelve studies for eight species (Lamniformes, n = 3; Carcharhiniformes, n = 5). PRS in studies ranged from 56% to 100%. Identifying causes for decreased PRS (i.e. mortality) was challenging for studies due to low sample sizes. Of the factors investigated, candidate best practices included: (1) using non-stainless steel circle hooks, (2) not removing sharks from the water, (3) reviving sharks prior to release, and (4) minimising time spent freeing the shark by removing the hook or cutting the line. With the conservation status of many sharks declining, more research is needed to strengthen the scientific basis for these practices to ensure that PRS in C&R is maximised.

1. Introduction

Sharks, skates and rays (Elasmobranchii) are an ecologically diverse group of Chondrichthyan fishes, comprised of over 1100 species (Weigmann, 2016) distributed throughout the world's oceans (Queiroz et al., 2019). Typically, sharks occupy high trophic levels (Bird et al., 2018) and play key roles in marine ecosystems, including top-down control of marine food webs (Baum and Worm, 2009), structuring fish assemblages (Klages et al., 2014) and scavenging dead or unfit individuals (Fallows et al., 2013). Sharks have *K*-selected life histories, characterised by slow growth, late maturation and long lifespans (Smith et al., 1998). These traits make sharks vulnerable to overexploitation and, as a result of persistent overfishing, global populations of many species have declined significantly (Pacoureau et al., 2021). Recreational angling (i.e. for sport or sustenance, as opposed to sale of meat and fins) is increasingly popular (Jones et al., 2021; Thomas et al., 2022) and accounts for ~1% of total fish catch globally, of which sharks account for ~5% (Freire et al., 2020). However, the often ad hoc nature of recording and reporting of recreational catches of sharks makes understanding the magnitude and effect of recreational fishing at population and ecosystem levels challenging (Lewin et al., 2019). Given their key ecosystem roles and susceptibility to overfishing, marine policy makers are increasingly looking to improve conservation of sharks (Davis and Worm, 2013; Sherley et al., 2020). Initiatives include legally binding agreements such as regulations on international trade through the Convention for International Trade in Endangered Species (CITES; e.g. oceanic whitetip, *Carcharhinus longimanus*), commercial catch prohibition (e.g. porbeagle shark, *Lamna nasus,* in waters of the European Union; EU, 2015), and mandates to land sharks with fins attached (e.g. EU regulation 605/, 2013 amending 1185/2003; EU, 2013). Non-binding agreements also exist, for example bycatch reduction protocols to increase discard survival in the commercial sector (Sepulveda et al., 2019; Zollett and Swimmer, 2019), and the

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implementation of voluntary or mandatory "catch-and-release" (C&R) practices in the recreational sector.

In C&R fisheries, fish are released back to the wild after angling (Gallagher et al., 2017a). The assumption for C&R fishing is that most released fish recover and survive. However, this may not always be the case, and, generally the survival of fish post-release has been shown to vary according to environmental conditions (Gingerich et al., 2007), and angling methods (see Bartholomew and Bohnsack, 2005 and Brownscombe et al., 2017 for general reviews). Survival also appears to be species specific (Musyl and Gilman, 2019), with some species, such as the great hammerhead shark (*Sphyrna mokarran*), exhibiting low post-release survivorship (PRS, e.g. in Gallagher et al., 2014 only 57% of 28 hammerhead sharks were considered to survive, whereas 100% of 28 tiger sharks, *Galeocerdo cuvier*, survived). The C&R angling sector has therefore developed an array of "best practices" to increase PRS (e.g. "use non-stainless steel circle hooks"). Due to inter-species differences in PRS, it has been proposed that best practices should be species-specific (Cooke and Suski, 2005), requiring research on the wide range of targeted shark species across representative habitats. To date, most science underpinning best practices for saltwater C&R angling has focused on teleost fish: bass (Fernholz et al., 2018; Lewin et al., 2018), salmonids (Roth et al., 2018), bonefish (Danylchuk et al., 2007), sturgeon (Struthers et al., 2018; McLean et al., 2020), istiophorid billfish (Musyl et al., 2015) and bluefin tuna (Stokesbury et al., 2011; Goldsmith et al., 2017; Sepulveda et al., 2020). While similarities between the responses of teleosts and sharks to C&R angling exist (e.g. a general increase in swimming speed post-release, Iosilevskii et al., 2022), key physiological (e.g. metabolic processes, Speers-Roesch and Treberg, 2010; Brill and Lai, 2015) and morphological differences (e.g. typically larger masses and greater prevalence of ram ventilation in sharks) may lead to differing responses of sharks to C&R when comparing with teleosts. For instance, in a commercial setting, Musyl and Gilman (2019) found that istiophorid billfishes (similar in mass to large-bodied sharks) were more robust to stressors sustained during capture, handling and release than pelagic sharks. Together these differences warrant an independent review of the response of sharks, specifically, to C&R.

Recently, research on the PRS of sharks has been identified as a priority (Gallagher et al., 2017a; Holder et al., 2020), leading to a number of studies in both recreational (Mohan et al., 2020; Nick Weber et al., 2020a; Anderson et al., 2021; Knotek et al., 2022a) and commercial fisheries (Ellis et al., 2017; Musyl and Gilman, 2019). Whilst there are some parallels between recreational and commercial fisheries (e.g. hook type), the capture experiences likely differ markedly in most cases. For instance, commercial captures typically occur over many hours (e.g. longline soak times, Campana et al., 2009) and can be passive captures where sharks can spend periods motionless whilst on the line (Knotek et al., 2022b). Recreational captures, in contrast, represent a dynamic interaction between the animal and the fisher, often termed a "fight", typically occurring over minutes (range between one and 14 min; Gurshin and Szedlmayer, 2004; Kneebone et al., 2013,2013b,2013c; Danylchuk et al., 2014,2014b,2014c; Weber et al., 2020; Knotek et al., 2022a) and can extend to hours in some cases (Heberer et al., 2010,2010b,2010c; French et al., 2015; Anderson et al., 2021). Moreover, recreational angling is highly variable in terms of gear and angler experience, which differs from commercial fishing where methods used are often more standardised. For this reason, we make a clear differentiation here between C&R science in recreational and commercial settings.

Here we review current research on shark C&R science and best practices with four key aims: (1) outline the underpinning science behind best practices, (2) identify areas where future research is needed, (3) suggest refinements in shark C&R science, and (4) recommend the most effective, universally applicable C&R best practices to increase PRS for sharks. To outline what best practice guidelines are available for anglers, we also conduct a review of available resources and bring these together as an online resource (www.sharks.sustainable-seas.org/global-guidelines) for ease of access.

2. Materials and methods

2.1. Catch-and-release literature

Structured searches of peer-reviewed scientific literature were conducted using Web of Science (Clarivate Analytics; https://www.webofknowledge.com) between May 2021 and August 2022. If literature was encountered outside of initial searches, search terms were broadened and repeated until all relevant studies were accounted for. The final search terms were combinations of: "catch", "release", "post-release", "postrelease", "behaviour", "sharks" and "shark" (126 publications returned, full list available as an online supplement). Studies that referred directly to the recreational angling process and that provided quantitative data relevant to assessing PRS were retained. Studies were then assessed based on six stages of a conceptual angling schematic outlined in Brownscombe et al. (2017): hooking, fight time, boarding, unhooking, handling time and recovery (Table 1). For each study, results pertaining to these angling stages were first assessed as present or absent. If results for a given stage were present, the effect of that stage (e.g. hooking) on PRS was noted as either positive, negative or having no effect. Individual shark data (i.e. total length, fight time, etc. for a specific animal) were compiled when available. Data including survival outcome were available for 208 individual sharks (i.e. tabulated in studies). However, statistical analysis of survival outcome against potential explanatory variables could not be conducted on these data due to problems associated with overfitting and small sample sizes (data were available for 27 mortalities from four species) resulting in bias and random errors (Harrell, 2015). When conducting logistic regressions that are used in survivorship analysis with sample sizes of less than ~10 mortality events per variable, the chances of Type I or II statistical errors occurring increases, outweighing the benefits of statistical testing (Peduzzi et al., 1995; Ogundimu et al., 2016). PRS is defined as the proportion of sharks (%) with stated outcomes that survived. This was calculated (1) for studies, (2) for species by pooling data for a given species (PRS_{ss}), and (3) for all sharks by pooling all available data (PRS_{total}). For pooled analysis of multiple species, data (e.g. length, fight time and handling time) were scaled by the mean in each study. Pooled data were analysed by angling stage using Kruskal Wallis non-parametric tests to test for differences in survival outcome and using a gaussian linear model to investigate the influence of shark body length on fight time. Differences in the proportion of sharks surviving different angling conditions (e.g. hook type) or with differing biological parameters (e.g. sex or body length) were investigated using a two proportion z-test with Yates' continuity correction. All errors reported are ± 1 standard deviation. In three instances data were unavailable for meta-analysis due to a lack of a data table (Kneebone et al., 2013,2013b, 2013c; Danylchuk et al., 2014,2014b,2014c; Kilfoil et al., 2017) and often some variables were not stated in data tables (e.g. body length or fight time). Inferences from these studies are still discussed but are not analysed explicitly. Box 1.

Table 1
Summary of stages of the angling process used to assess and summarise studies. Angling stages (i.e. Action) taken from Brownscombe et al. (2017) and associated variables adopted from scientific literature.

Stage	Description (unit)
Hook	(1) Type – e.g. circle or "J", or, (2) hooking location.
Fight time	The duration of time between the shark biting the hook and being physically restrained at the vessel. (Minutes)
Boarding	Was the shark boarded or not? (Yes | No)
Unhooking	Was the hook removed or left in? (Yes | No)
Handling time	The duration of time between physically restraining the shark post-"fight" and releasing the shark back the wild. (Minutes)
Recovery	Was the shark revived or not? (Yes | No)

Box 1
Terminology.

In the following text we refer to 'best practice', understanding that there is likely no single best approach that would optimise PRS for all shark species. We recognise that guidelines for best practice reflect a continuous progression of understanding and are re-published at discrete time points. Here 'guidelines' refer to a single document (online or in-print) published somewhere visible to the wider angling community, containing multiple best-practices considered together. For examples of guidelines included in this manuscript, see our global synopsis of catch and release best practices at www.sharks.sustainable-seas.org/global-guidelines.

2.2. Best practice guidelines

We conducted structured online searches using Google for shark C&R best practice guidelines from Governmental and interest organisations (e.g. from the National Oceanic and Atmospheric Administration). Country-specific searches were conducted using "[*country*]" and "recreational shark [fishing or angling] guidelines" or "recreational shark [fishing or angling] best practices". The first 20 results returned by Google were scanned and guidelines were saved if they were either (1) shark-specific, or, (2) were not shark-specific but referred to sharks in the text. Acknowledging that the search terms biased the results to English speaking countries, we also conducted searches using Google in Italian, Portuguese, French and Spanish reflecting languages spoken in areas where recreational shark fishing is most practiced (*as per* Gallagher et al., 2017). Published guidelines consisted of a number of individual practices (e.g. "use a circle hook"). Once identified, documents were evaluated against 17 individual practices for catching and releasing sharks in recreational activities compiled by Gallagher et al. (2017; Table 2). Individual guidelines were scored out of 17 based on whether practices identified by Gallagher et al. (2017) were present or absent (i.e. 0 = no practices present, 17 = all practices present), and summed across guidelines and angling stages (pre-angling, gear, capture, handling, and release; Table 2).

3. Results and discussion

3.1. Catch-and-release science

To date, C&R research for sharks is limited to 12 studies on eight species, from two of eight extant orders of sharks (Lamniformes, n = 3; Carcharhiniformes, n = 5; Fig. 1, Table 3). By contrast, at least 28 shark species are targeted by recreational anglers in the USA alone (Mcclellan Press et al., 2016). Studies have been conducted in the North Atlantic (n = 6), Gulf of Mexico (n = 4), North Pacific (n = 2) and South Pacific (n = 2; Fig. 1). Overall, the geographic range of C&R research remains limited with all but two studies to date conducted in the USA, and the other two in Australia and the Bahamas. Of 396 sharks that were followed after angling over 12 studies (33 ± 21 sharks per study, range = 10–81), 334 survived (PRS_{total} = 84%) and 63 died. Study specific PRS ranged from 56% to 100% (Table 3) and species-specific mean PRS_{ss} ranged from 65% in common thresher shark (*Alopias vulpinus,* n = 36 sharks) to 100% in porbeagle shark (n = 13 sharks). Detailed information at the individual level could only be tabulated for 208 sharks (53% of the 396 studied) from 9 studies (75%), which included 27 mortalities (13%) for five species.

Sharks targeted in recreational fisheries span a broad range of body types and sizes, from small-bodied demersal sharks (e.g. juvenile lemon shark *Negaprion brevirostris*, min. size 0.53 m Total Length, TL; Danylchuk et al., 2014,2014b,2014c) to large-bodied pelagic sharks (e.g. tiger sharks, max size 5 m TL; Gallagher et al., 2016). Studies represented an average of 53 ± 18% of each study species' size range (i.e. total body length, range 26–91%), and over 39 ± 20% of their thermal niche (range 14–95%; Fig. 2). Fight time and hooking have so far been the most investigated influencing factor in PRS (each 83% of studies, n = 10, Table 1; Fig. 3), followed by handling (42% of studies, n = 5) boarding and unhooking (each 33% of studies, n = 4). Only one study considered pre-release recovery in its experimental design (Weber et al., 2020). In addition to the effect of angling on PRS, 67% of studies (n = 8) also investigated the physiological disruption caused by angling by measuring blood biochemistry. Of the six stages of angling outlined by (Brownscombe et al., 2017), most studies considered an average of just 3 ± 2 stages (range 1–6, Fig. 3). Importantly, only eight studies had the sample size or statistical power to underpin their findings with statistical testing, with other inferences being based on circumstantial evidence.

Studies applied numerous techniques to obtain PRS estimates, including surface tracking using fishing floats (Danylchuk et al., 2014,

Table 2
Best practices for catching and releasing sharks in recreational angling activities proposed by Gallagher et al. (2017). * * Denotes a term not used by Gallagher et al., but that was included as a variable in several of the assessed studies. Emboldened text highlight practices derived from Table 2 and used in Fig. 3.

Angling Stage	Practice
Be prepared (pre-fishing)	1. Avoid fishing in warmer waters that tend to have lower dissolved oxygen and make recovery more difficult.
	2. Avoid fishing in silty water that can clog shark gills.
	3. Have appropriate release gear before recreational fishing.
	4. Make sure members of fishing team understand their roles in release.
Gear	**5. Use circle hooks to reduce deep hooking. ("Hook type or location";Fig. 3)**
	6. Use corrodible non-stainless hooks.
	7. Use barbless hooks for faster removal.
	8. Use heavy tackle and fight harness to minimize fight time.
Capture	**9. Minimize fight time to reduce exhaustion and stress ("Fight time";Fig. 3)**
	10. Avoid foul-hooking sharks.
	11. Follow hooked sharks to gain line and reduce fight duration.
	12. If species captured is known to be sensitive to capture stress (e.g. hammerhead and, thresher sharks), then cut line immediately after trying to gain as much line as possible back in a short time.
Handling	13. Do not gaff sharks.
	14. Do not remove sharks from water. ("Boarding";Fig. 3)
	* ***Minimise time between subduing shark and release. ("Handling";Fig. 3)**
Release	**15. Resuscitate exhausted shark prior to release by keeping water flowing through mouth and over gills. ("Recovery";Fig. 3)**
	16. Maintain mouth against current direction or always keep shark in forward direction (do not motion both forward and backward like teleosts).
	17. Remove hook/line by (1) cutting hook with bolt cutters/de-hooker; (2) cutting line as close to hook as safely possible. ("Unhooking";Fig. 3)

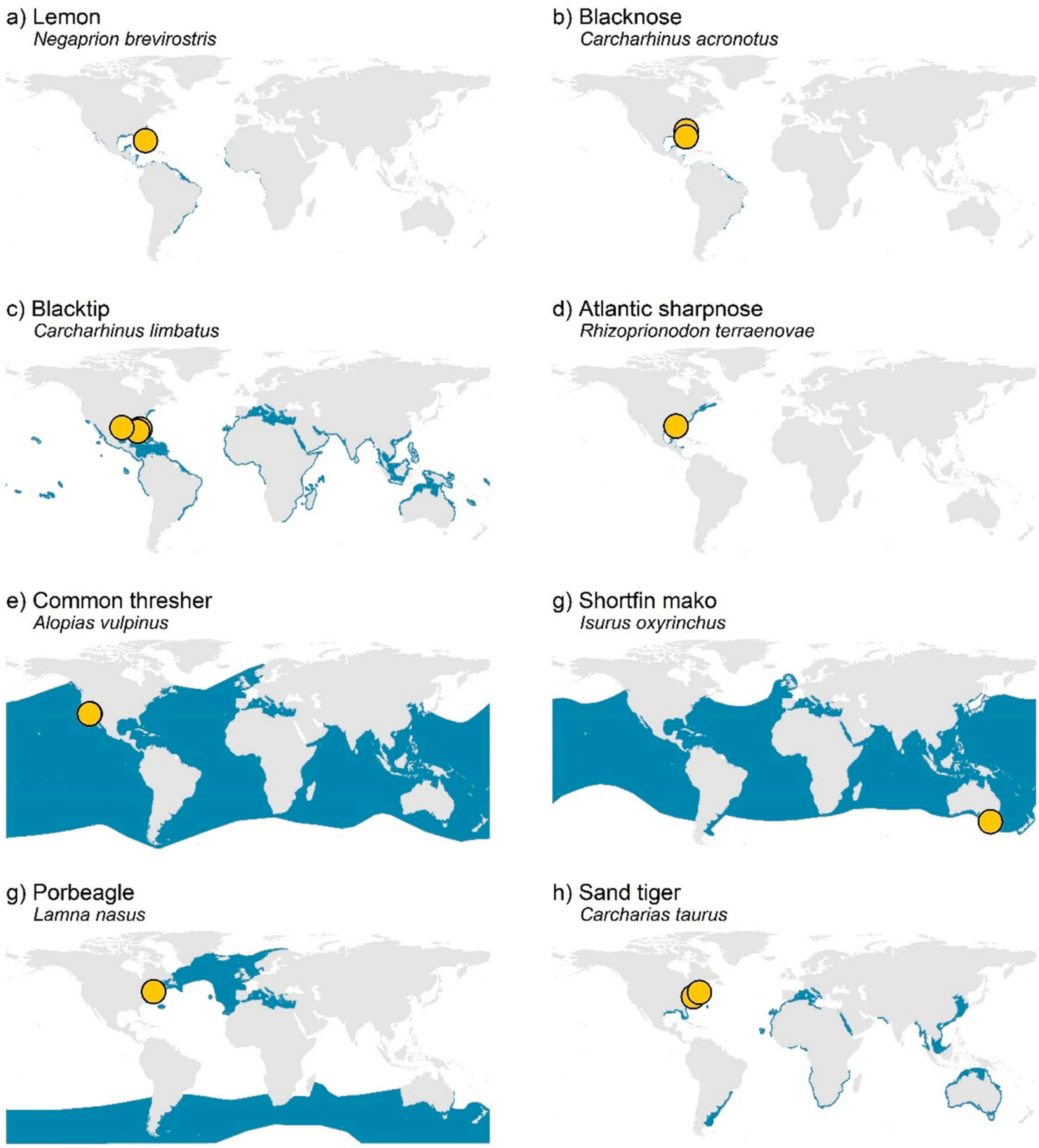

Fig. 1. Geographic distribution of shark catch-and-release studies. Blue shaded area denotes the known geographic range of studied sharks (reproduced with permission from the International Union for the Conservation of Nature and available at https://www.iucnredlist.org/). Yellow filled circles denote individual study locations.

2014b,2014c) or acoustic telemetry together with a directional hydrophone (Gurshin and Szedlmayer, 2004), tracking using moored acoustic telemetry systems (Kneebone et al., 2013,2013b,2013c; Kilfoil et al., 2017; Weber et al., 2020), pop-up satellite archival tags (Heberer et al., 2010,2010b,2010c; French et al., 2015; Sepulveda et al., 2015; Mohan et al., 2020; Weber et al., 2020; Anderson et al., 2021) and sub-second behaviour using accelerometery tags (Whitney et al., 2017; Knotek et al., 2022a). Experimental methods differed, and studies followed sharks for time periods between 15 min and 180 days post-release (Table 3). As a result, most studies estimated acute PRS (up to 10 days post-release), while only five studies were able to provide longer term estimates of PRS (over a period of up to 180 days; Table 3). A tracking period of 24 h may be sufficient to discern immediate mortality (Whitney et al., 2016a), with 64% of studies (n = 7 of 11 studies where mortalities were recorded) recording mortalities within the first 24-hours post-release. However, mortalities also occurred after 81 days for common threshers trailing fishing gear (Sepulveda et al., 2015) and 90 and 31 days for juvenile (Kneebone et al., 2013,2013b,2013c) and adult sand tiger sharks, *Carcharias taurus,* respectively (Kilfoil et al., 2017). However, the protracted period between release and mortality make it challenging to link delayed mortality directly to angling. Regardless, studies actively following sharks for less than 24 h likely underestimated immediate mortality (Gurshin and Szedlmayer, 2004; Danylchuk et al., 2014,2014b,2014c) and studies following sharks for less than 90 days (n = 7) may underestimate long-term mortality. However, with only three mortalities recorded after this period, it is still challenging to make robust recommendations about the minimum periods that should be recorded. Of the 27 shark mortalities that were recorded, sharks were identified as dead if they stopped moving, sank or were depredated. However, of the three studies that recorded

Table 3
Post-release survivorship estimates for C&R angled shark species. For PRS type, "Acute" is defined as estimates of PRS that did not take into account delayed effects of capture on PRS, whereas "Long-term" denotes PRS estimates that accounted for both acute (<10 days post-release) and delayed (10 days or more post-release). Emboldened PRS values are repeated in Fig. 3.

Common species name (scientific name)	Study and Geographic Area	Size (TL, mean ± 1 S. D.)	PRS (n = number of individuals)	PRS type	Description
Lemon (*Negaprion brevirostris*)	Danylchuk et al. (2014) *North Atlantic*	68 ± 8 cm (53–88 cm)	**86% (n = 32)**	Acute	< 15 min post-release. Assessed by tracking sharks in-situ using surface markers.
Blacknose (*Carcharhinus acronotus*)	Knotek et al. (2022) *Gulf of Mexico / North Atlantic*	99 ± 8 cm (83–119 cm)	**91% (n = 47)**	Acute	Acceleration data-loggers were used to monitor sharks for 0.6–136 h post-release
Blacktip (*Carcharhinus limbatus*)	Whitney et al. (2017) *Gulf of Mexico / North Atlantic*	108 ± 11 cm (92–132 cm)	**90% (n = 31)**	Acute	Acceleration data-loggers were used to monitor sharks for 7–72 h post-release
	Mohan et al. (2020) *Gulf of Mexico*	111 ± 10 cm (89–134 cm)	**77% (n = 22)**	Long-term	Tags were programmed for 30- (sPAT) or 180-day (MiniPAT) deployments. Five sharks died within 14 h post-release and 17 survived.
	Weber et al. (2020) *Atlantic*	124 ± 19 cm (range not provided)	83% (n = 41)	Long-term (shore-angled)	All sharks were outfitted with a V16–4 H (VEMCO) acoustic tag and a subset (n = 12 shore-angled; n = 12 boat angled) were double tagged with a PSAT (PSATLIFE, Lotek – 28 d pop-up) to validate results. Fifteen sharks died within 10 days of release. No sharks were classed as moribund on release and 7/15 sharks that died were assigned a release condition of either excellent (n = 6) or good (n = 1).
			80% (n = 40)	Long-term (boat-angled)	
			82% (n = 81)	Long-term (combined)	
Atlantic sharpnose (*Rhizoprionodon terranovae*)	Gurshin et al. (2004) *Gulf of Mexico*	81 ± 12 cm (67–100 cm)	**90% (n = 10)**	Acute	Tracked continuously after release using ultrasonic telemetry for periods of 0.75–5.90 h. Positions recorded at a median interval of 9 min
Common thresher (*Alopias vulpinus*)	Heberer et al. (2010) *North Pacific*	185 ± 17 cm (160–221 cm)	**74% (n = 19)**	Acute	Tags (MK10s) were programmed for 10-day deployments. 5 sharks died within 4 h of release and 14 survived 10 days at liberty
	Sepulveda et al. (2015) *North Pacific*	146 ± 20 cm (111–187 cm)	100% (n = 7)	Acute (mouth-angled)	Tags (MK10s) were programmed for 10-day deployments. No sharks died in the study period.
			22% (n = 9)	Long-term (tail-angled)	Tags (MK10s) were programmed for 90-day deployments. 5 sharks died within 24 h and one after 81 days.
			63% (n = 16)	Long-term (combined)	All angling categories
Porbeagle (*Lamna nasus*)	Anderson et al. (2021) *Northwest Atlantic*	122 ± 39 cm (88–209 cm)	**100% (n = 13)**	Long-term	Tags were programmed for a range of deployment lengths between 28 days and 9 months (Lotek PSATLIFE tags, 28 d; n = 7; sPATs, 30 d, n = 4; and Microwave Telemetry X-Tags - High Rate, 30 d, n = 1; and, Standard Rate, 9 mo, n = 2). No sharks died post-release and behaviour was inferred from diving behaviour.
Shortfin mako (*Isurus oxyrinchus*)	French et al. (2015) *South Pacific*	176 ± 37 cm (110–265 cm)	**90% (n = 30)**	Long-term	Tags (sPATs) were programmed to report after 30 days. All mortalities occurred within 24 h post-release.
Sand tiger (*Carcharhinus taurus*)	Kneebone et al. (2013) *North Atlantic*	92 ± 9 cm (78–120 cm)	99% (n = 66)	Acute	< 5 days post-release. Assessed using acoustic tag and passive monitoring. One shark assumed to have died post-release.
			82% (n = 66)	Long-term	5 to < 50 days post-release. Assessed using acoustic tag and passive monitoring. Cumulative total of 8 sharks assumed to have died.
			75% (n = 60)	Synoptic	50–100 days post-release. Assessed using acoustic tag and passive monitoring. Cumulative total of 15 sharks assumed to have died.
	Kilfoil et al. (2017) *North Atlantic*	200 ± 23 cm (146–246 cm)	**94 (n = 35)**	Long-term	Assessed using acoustic tags. Sharks that moved throughout the array were classified as alive whereas those that were detected at a single location for ≥ 24 h with no subsequent movements were considered to have died. Individuals that left the array and were no longer detected were considered to have survived.

post-release depredation, two included these mortalities in PRS estimates (Weber et al., 2020; Knotek et al., 2022a) and one did not (Mohan et al., 2020). Overall, our ability to understand the causes of post-release mortality and predict outcomes of angling remains limited.

3.2. Disruption of blood chemistry

When caught by an angler, a shark experiences a series of physiological changes whilst attempting to flee (the fight), being subdued (handling) and then prior to release (revival; Renshaw et al., 2012). Physiological stress responses in fish are mediated by catecholamines and corticosteroids (Skomal and Mandelman, 2012). While catecholamines are the same in teleosts and elasmobranchs, the primary corticosteroid in teleosts is cortisol, which is absent in elasmobranchs; Instead, 1α-hydroxycorticosterone (1α-OHB) is thought to play a similar role in elasmobranchs (Hazon and Balment, 1998). Measuring 1α-OHB is, however, challenging, and secondary compounds have been sampled instead to understand physiological disruption in sharks (Skomal and Mandelman, 2012). The challenge is how to relate physiological disruption to PRS, since once released, sharks are rarely resampled

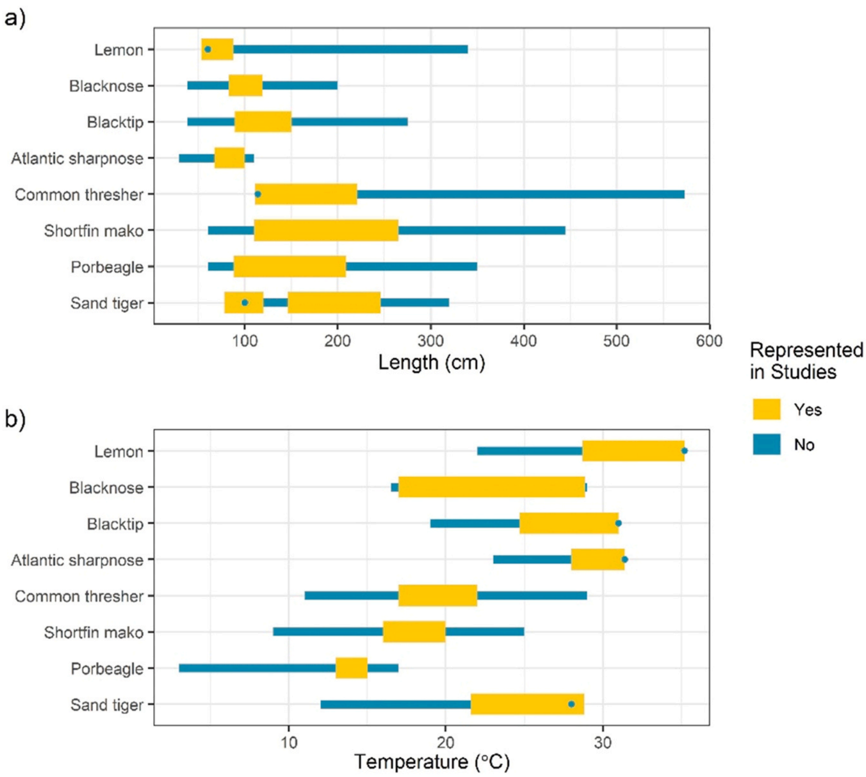

Fig. 2. Representation of (a) species body length and (b) species thermal ranges in shark C&R published literature. Body length and thermal niche sourced from FishBase.org and based on minium and maximum values. Blue dots represent FishBase minima and maxima if obscured by species data.

(Jerome et al., 2018). Overall, blood metabolites investigated in eight studies were not found to be directly related to PRS, but some general trends associated with angling phases existed. During the fight, sharks increase muscle force from maximal to supramaximal output using anaerobic respiration and hence produce lactate, which increases in concentration with fight time (Heberer et al., 2010,2010b,2010c; Kneebone et al., 2013,2013b,2013c; Danylchuk et al., 2014,2014b, 2014c; French et al., 2015; Whitney et al., 2017; Mohan et al., 2020). While at supramaximal metabolic rate, lactate causes acidosis of the blood (Robergs et al., 2004). The physiological fight capacity of a shark is influenced by the ratio of body oxygen (O_2) stores (myoglobin, haematocrit and haemoglobin) to O_2 consumption rate, and the capacity to oxidise metabolic by-products, such as lactate. High levels of blood lactate have been linked to mortality for commercially captured blue (*Prionace glauca*) and shortfin mako sharks (Isurus oxyrinchus, Moyes et al., 2006; Marshall et al., 2012) and blacktip (*Carcharhinus limbatus*) and spinner sharks (*Carcharhinus brevipinna*, Whitney et al., 2021). However, only one study reported a statistically significant relationship between blood lactate and PRS in the recreational sector, with surviving sharks having significantly lower lactate and blood pH than those that died (Mohan et al., 2020). Blood lactate concentration was positively related to fight time in seven studies, and to handling time in another study (lactate values ranged from nearly 0–33.8 mM L^{-1}; Fig. 3).

The accumulation of intramuscular metabolic end products through protracted anaerobic glycolysis (i.e. after longer fight times) can lead to irreversible cell damage in sharks and possibly death (reviewed by Skomal and Mandelman, 2012). Research to date suggests that this physiological endpoint may be less likely to be met in recreationally fished sharks (Shea et al., 2022) compared to commercially fished sharks, where physiological endpoints can reliably predict survivorship (Marshall et al., 2012; Whitney et al., 2021). Instead, lactate acts primarily as a correlate for fight time and may be a poor indicator of PRS in C&R fisheries. Blood lactate levels as high as 38.8 ± 13 mmol L^{-1} have been reported for blacktip sharks captured commercially (mean ± SD; Marshall et al., 2012), whereas a maximum of 8 mmol L^{-1} has been recorded for recreationally captured blacktip sharks (Mohan et al., 2020). In adult male blue sharks, blood lactate, pH, glucose, calcium (Ca^{2+}), phosphate (PO_4^{3-}), and potassium (K^+) are reported as unaffected by fight time, which is commonly shorter than 30 min (Shea et al., 2022). Blood K^+, PO_4^{3-}, sodium, creatinine, chloride, magnesium, pH, haematocrit, and calcium were shown to be significantly related to fight time in other studies conducted on sand tiger, lemon, and blacktip sharks (Kneebone et al., 2013,2013b,2013c; Danylchuk et al., 2014, 2014b,2014c; Weber et al., 2020); and handling time was negatively related to haematocrit and blood pH in two studies on blacktip sharks (Whitney et al., 2017; Mohan et al., 2020). In most cases, however, the authors found it challenging to determine what the significance of these changes might be for PRS. While the relationship between many of these metabolites and stress (and PRS) is understood in teleost fish, their baseline concentration differs between elasmobranchs and teleosts due to differences in metabolism (Speers-Roesch and Treberg, 2010) and osmotic and ionic regulation (Skomal and Mandelman, 2012). As such, relationships between blood electrolytes and stress described for teleosts cannot be readily applied to C&R studies of sharks. Finally, it could be that physiological disruption in angled sharks seldom reaches critical points that lead to mortality shortly after capture, but further research would need to be conducted to assess this.

Behavioural impairment that does not directly lead to mortality may, however, lead to an increased risk of depredation in areas where predators are common, such as the southeastern coast of the United States (Mohan et al., 2020; Weber et al., 2020; Knotek et al., 2022a). Using accelerometers, Knotek et al. (2022) and Whitney et al. (2017) note that sharks exhibited increased tail beat frequency immediately post-release, taking 11.7 ± 4.5 h and 11 ± 2.6 h to recover "normal", or steady-state, swimming behaviour (right-side asymptote of monitoring period as detailed in Whitney et al., 2016). Depredation of released sharks occurred within this recovery period, which could indicate that sharks may be easier prey when recovering from a C&R event, despite

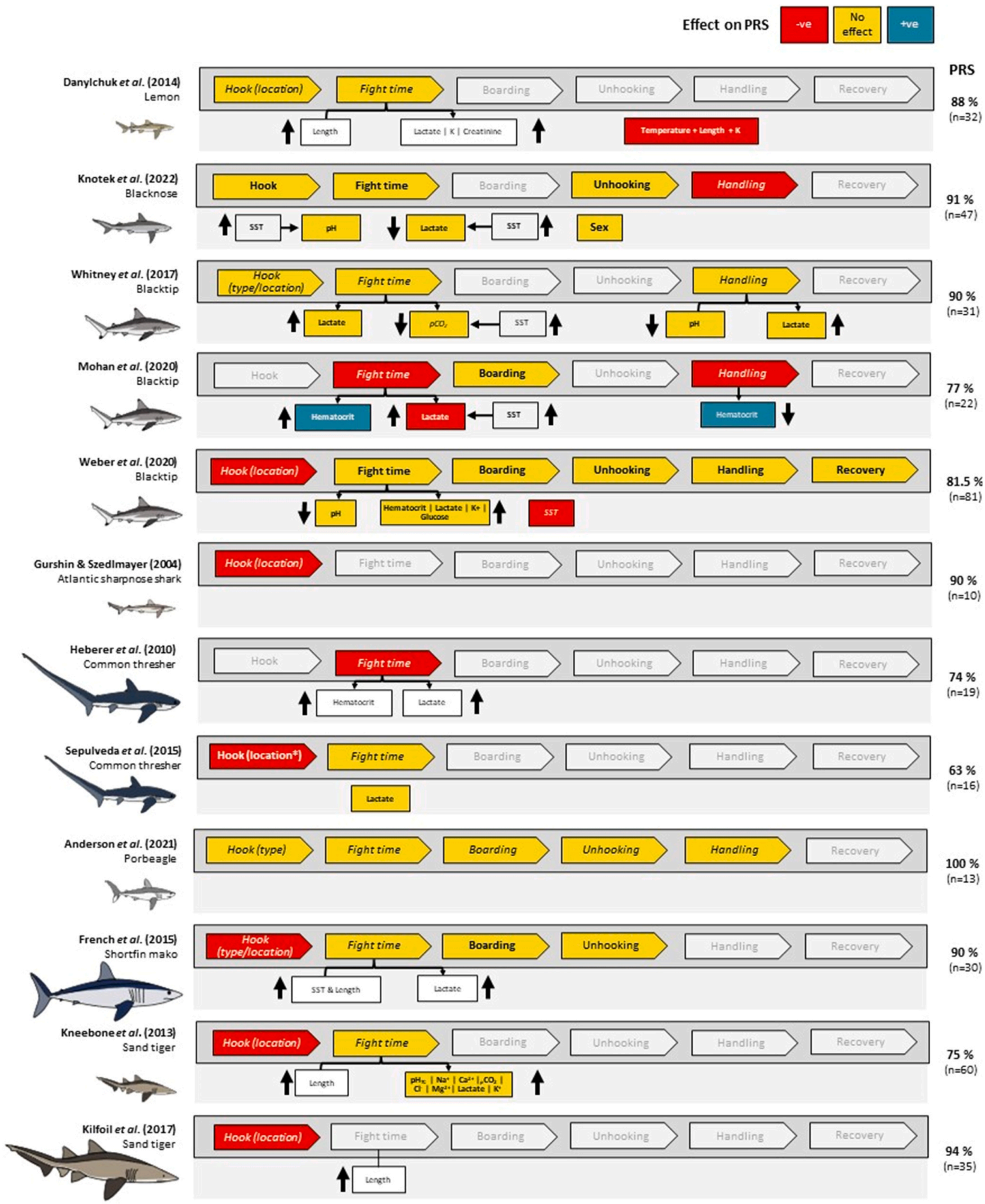

Fig. 3. Recreational fishing effects on post-release survivorship of shark species. Flow diagrams (filled arrows) representing the recreational fishing process (Table 1) and relevant environmental and physiological factors influencing post-release survivorship (PRS). Coloured horizontal filled arrows represent effects of angling stages on PRS (relationship and directionality). Greyed out arrows denote steps that were not explicitly examined by publishing authors. Bold text represents stages where effects are underpinned by statistical testing ($p = < 0.05$) and italic text represents stages steps with only circumstantial evidence of effect. Braces connecting respective variables denote relationships and arrows by the side of boxes indicate direction of the effect ($p = < 0.05$). Quoted PRS values are explained in Table 2 and "n" refers to the number of individual sharks in PRS calculation. Size of shark illustrations indicative of differences in body length between individuals represented in studies. SST – Sea Surface Temperature. Sorting on y-axis is by taxonomical group.

swimming faster (due to the increased tail beat; Mohan et al., 2020; Weber et al., 2020; Knotek et al., 2022a). Increased risk of depredation does not appear to contribute to PRS estimates for lamnid sharks (Heberer et al., 2010,2010b,2010c; French et al., 2015; Sepulveda et al., 2015; Anderson et al., 2021), most likely due to their larger size and possible lack of predators at tagging sites.

3.3. Effects of angling stages on survivorship

For the purposes of this review, we consider effects on PRS of animal size, ambient temperature and events at six angling stages: hooking (hook type and hooking location), fight time, boarding, unhooking, handling time and whether sharks were revived (Fig. 4).

3.3.1. Hooks (type, location and removal)

Fishing hooks create physical trauma, and hooking location appears to be a determinant of injury severity for sharks, with sharks that are 'deep hooked' (i.e. the hook isn't easily visible in the mouth) exhibiting injuries more likely to cause mortality than those hooked in the mouth (Gurshin and Szedlmayer, 2004; Campana et al., 2009; Kneebone et al., 2013a,2013b,2013c; French et al., 2015; Sepulveda et al., 2015; Kilfoil et al., 2017; Weber et al., 2020). Using circle hooks (as opposed to j-hooks) decreases hooking-related injuries in both commercial (Reinhardt et al., 2018) and C&R fisheries (Cooke and Suski, 2004) through promoting mouth-hooking, and their use is often seen as a refinement to increase PRS in C&R fisheries. In total, 178 shark captures in our review (of 396) had data on hook types with a survival outcome, with a significantly higher proportion of circle-hooked sharks surviving than j-hooked sharks (circle = 90% survival, n = 90; j = 60% survival, n = 60; two proportion z-test with Yates' continuity correction, $\chi^2 = 7.3$, p = 0.007). Of these 178 sharks, 131 also had information on hooking location (74%; Fig. 5). A significantly higher proportion of sharks angled with circle hooks were hooked in the mouth (88%, n = 49) than those angled with j-hooks (39%, n = 31; two proportion z-test with Yates' continuity correction, χ^2 =29.7, p = <0.001). Research indicates that the efficacy of circle hooks in hooking in the mouth and increasing PRS is species-specific. For instance, Kilfoil et al. (2017) found that circle hooks did not reduce incidence of deep hooking for sand tiger sharks (60% and 54% of angled sharks hooked in the gut with j- and circle hooks, respectively) and that deep-hooking, even with circle hooks, was a likely candidate for observed mortalities. This outcome is related to the gulp feeding habit of sand tiger sharks whereby prey is often consumed whole, leading to elevated deep hooking rates (Lucifora et al., 2009). To the contrary, a higher proportion of shortfin mako sharks were hooked in the jaw when using circle hooks in comparison to j-hooks (French et al., 2015), with sharks angled with circle hooks considered more likely to survive. Whilst not directly comparable (due to a range of differences in techniques and handling), these species-specific findings are similar to results in commercial settings, where circle hooks reduce hooking injuries and/or mortality for oceanic whitetip (*Carcharhinus longimanus*), scalloped hammerhead (*Sphyrna lewini*) and shortfin mako sharks (Reinhardt et al., 2018), but not necessarily for other species including blue, bigeye thresher (*Alopias superciliosus*) and porbeagle sharks (though did not increase it either, Reinhardt et al., 2018).

Angled sharks are sometimes hooked externally on the body ('foul hooked'), for instance in the tail (Heberer et al., 2010,2010b,2010c; Sepulveda et al., 2015; Weber et al., 2020), which results in them being retrieved backwards to the vessel. Tail-hooked sharks (common thresher and blacktip) had lower PRS (PRS = 71%, n = 15, but decreasing to 22% if terminal tackle, such as hooks and weights, were left embedded in the caudal fin, "trailing gear", Sepulveda et al., 2015) than sharks that were hooked in the jaw (PRS = 91%, n = 70). In contrast to teleosts, most sharks are obligate ram-ventilators, and cannot maintain water flow over their gills to breathe when moving backwards. Moving backwards leads to hypoxia and, ultimately, asphyxiation. Tail hooking has been shown to cause mortality for both common thresher (Heberer et al., 2010,2010b,2010c; Sepulveda et al., 2015) and blacktip sharks (Weber et al., 2020), but is particularly common in thresher sharks (*Alopias* spp.) due to their characteristic feeding behaviour whereby they use their tail to stun prey (Aalbers et al., 2010). Although tail hooking is less common in other shark species, wrapping of the line around the tail ("tail-wrapping") can occur in all angled sharks, also resulting in individuals being retrieved tail-first. This has been shown to cause mortality in blacktip sharks (Weber et al., 2020) and Atlantic bluefin tuna (*Thunnus thynnus,* Stokesbury et al., 2011). Consequently, angling practices that promote hooking in the mouth (and avoid hooking in the tail or gut) and avoid tail wrapping may be candidate best practices. Circle hooks may aid in reducing foul-hooking in commercial fisheries (Epperly et al., 2012), but whether they also reduce foul hooking in a recreational setting is unknown and requires further research. Tail wrapping is thought to occur mostly due to angler error, by allowing slack in the fishing line during the fight, leading to the line cinching around the tail while the animal is swimming away (Stokesbury et al., 2011). In practice, anglers may be able to reduce the risk of this happening by maintaining constant pressure between angler and fish to reduce slack. Given that species specific feeding habits for both sand tiger and common thresher sharks result in hooking locations that may increase mortality in recreational fisheries, the feeding behaviour of the target species should also be considered when choosing angling methods and locations.

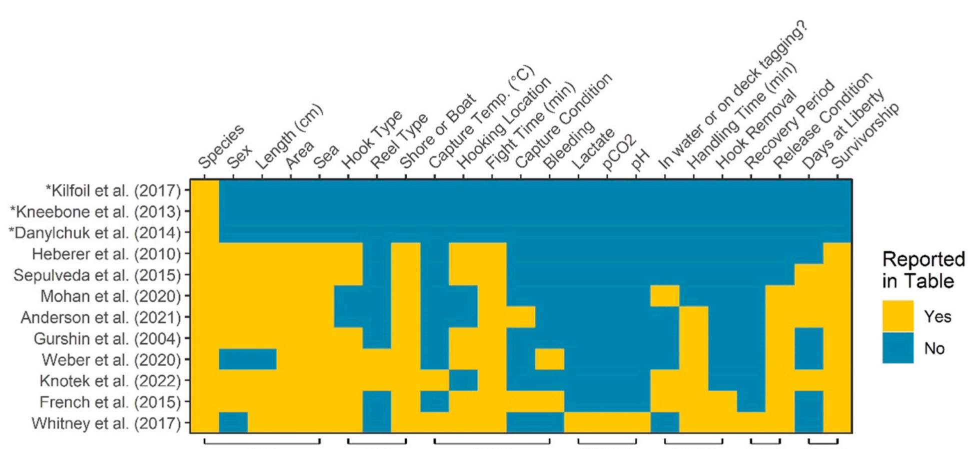

Fig. 4. Summary of data available at the level of individual shark tabulated from published literature. Asterisks denote studies that did not provide a data table in any form. For these studies all reported information was gathered from text. Sorting on y-axis is by summed number of data categories for each study from most (bottom) to least (top).

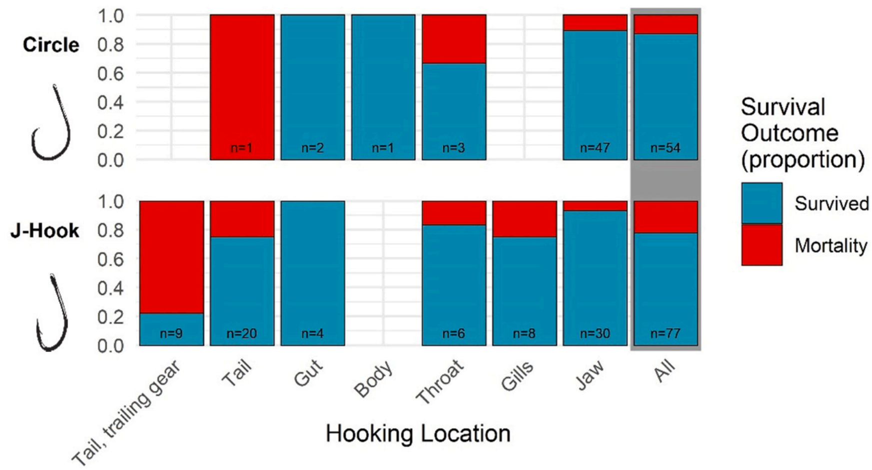

Fig. 5. Meta-analysis of post-release survivorship in relation to reported hook type and hooking location. Sample size for each group is given at the bottom of each respective bar.

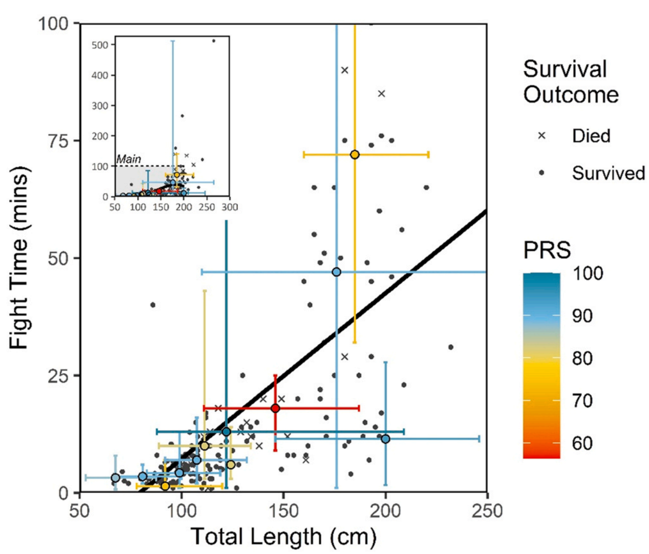

Fig. 6. Relationship between total length and fight time with corresponding PRS values. Coloured scatterplot shows mean values for ten of twelve studies evaluated. Error bars denote the range of values reported by each study. Black bold line denotes linear model. Values for individual sharks tabulated in studies are plotted as small black points, with point shapes denoting the survival outcome of that individual. Inset plot shows the full range of data.

Retained fishing hooks in sharks have the potential to cause pericarditis and peritonitis, affecting the health of the animal (Borucinska et al., 2001). However, sharks with retained fishing hooks have been found to have normal body mass, potentially indicating normal feeding behaviour whilst carrying a retained hook (Borucinska et al., 2002). Direct observations of animals with retained hooks post-release are valuable to reveal how hooks left in situ after C&R fishing may affect PRS. From the work reviewed here, there is insufficient evidence to demonstrate whether removal of hooks prior to release improves PRS. Removing the hook prior to release was considered by four studies (n = 104 sharks; Fig. 8) and did not appear to affect PRS. Whilst data were not available for all four studies, indications from Weber et al. (2020) and French et al. (2015) suggest no effect whereas Kilfol et al. (2017) suggest that sharks that died had hooks in situ at release. Hook removal after angling is a trade-off between the perceived benefit of removing the hook and the detriment of the extra handling required to remove it. Detrimental effects of de-hooking may range from superficial injuries, as seen in teleost fishes (e.g. if anglers are inexperienced or if sharks are particularly active during restraint, Brownscombe et al., 2017) to chronic effects arising from protracted air exposure (i.e. hypoxia) or serious trauma to vital structures (Cooke and Danylchuk, 2020). In some circumstances, the likelihood of increased stress and injury during hook removal may be sufficiently great that cutting the leader and leaving the hook in situ is the preferred option (French et al., 2015; Kilfoil et al., 2017; Weber et al., 2020; Anderson et al., 2021). A good example of this is for sand tigers, whereby the hook is often set in deep tissues and cannot be removed without causing further damage (Lucifora et al., 2009; Kilfoil et al., 2017). The counter-argument to leaving hooks in situ as standard is the potential for long-term mortality due to poisoning or infection, or through changes to feeding or reproduction (McLoughlin and Eliason, 2008). There are limited data to inform this understanding because (1) many studies were only able to cover relatively short time spans (< 30 days post-release; Table 3) and injuries caused by hooking may take longer to result in mortality, and (2) most sharks (n = 373, 94%) were not resampled to be able to assess wounds at the hooking site. Recent research on tiger sharks off Tahiti, French Polynesia showed that (1) non-stainless steel hooks left in place were shed within 2.5 years (whereas stainless hooks persisted for up to 7.6 years), and, (2) sharks carrying hooks and trailing line, showed no signs of growth impairment (Bègue et al., 2020). Thus, while it seems appropriate to remove hooks from sharks after angling (as suggested by most best practice guidelines), more research should be directed to understanding the trade-off between the detrimental effects of prolonged handling compared to leaving the hook in place.

3.3.2. *Fight time*

Minimising the time taken to bring fish to the catch boat, i.e. the "fight time" is a widely accepted method for minimising capture related stress (Cooke and Suski, 2005), and was closely observed in all studies reviewed. During the fight there is an increased risk of hypoxia caused by entanglement (Stokesbury et al., 2011), depredation by other animals (Mitchell et al., 2018) and physiological disruption due to exhaustive exercise (Renshaw et al., 2012). Hence, shorter fight times are generally associated with increased PRS, while extended fight times are often associated with increased mortality risk (Cooke and Suski, 2005). Direct, statistically significant, evidence of a negative effect of prolonged fight time on PRS is, however, lacking. Instead, research has suggested that longer fight (in recreational settings) or capture times (in commercial settings) may not always translate into higher stress levels (Gallagher et al., 2014, 2019; Musyl et al., 2015; Tate et al., 2019; Shea et al., 2022). This response is likely to be species-specific (Jerome et al., 2018)

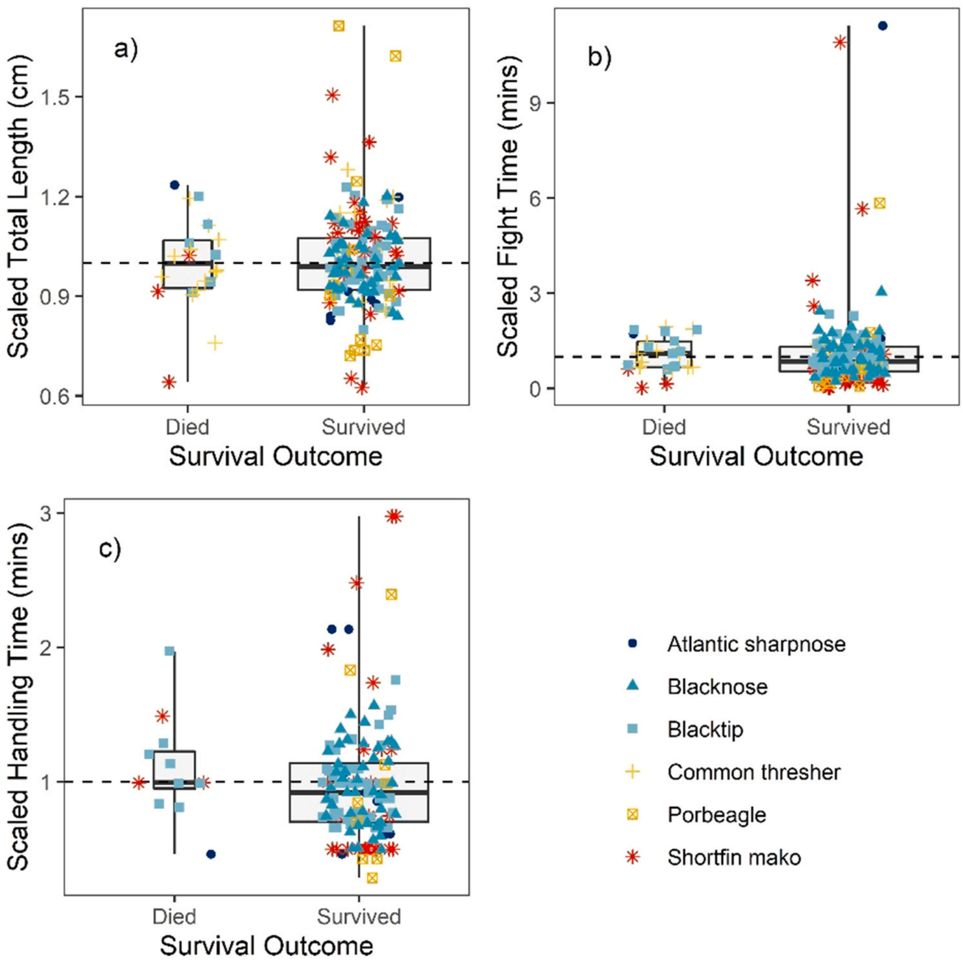

Fig. 7. Effect of total length, fight time and handling time on post-release survivorship for sharks in all studies providing individual tabulated shark data. Data are scaled by dividing values by the study-wise mean. Horizontal dashed line represents values that equal the mean. Raw data are overlaid using a random scattering to avoid overplotting.

due to differences in exertion between species (Gallagher et al., 2017b). In the studies we reviewed, sharks that died were not fought for longer than sharks that survived (Kruskal Wallis, $n = 204$, $\chi 2 = 2.514$, $p = 0.06$). There was a positive correlation between shark body length and fight time, explained as log(Fight Time (mins)) = −0.64 + 0.022 x Total Length (cm; linear model, $n = 180$, $t = 17.4$, $p = <0.001$; Fig. 6), and sharks that died were not larger than sharks that survived (Kruskal Wallis, $n = 140$, $\chi 2 = 0.007$, $p = 0.9$). This latter result is perhaps unsurprising given the covariance of shark body length and fight time. Thresher sharks represent an exception, with tail-hooked smaller sharks having shorter fight times and higher survival rates (Heberer et al., 2010,2010b,2010c). In this case, an increase in fight time would translate to a longer period of asphyxiation. Whitney et al. (2017) note that time to recover normal behaviour was negatively correlated with shark body length in blacktip sharks, despite larger sharks being angled for longer. For recreationally captured blue sharks, research has also demonstrated that smaller sharks may be more susceptible to capture stress, despite having shorter fight times than larger individuals (Shea et al., 2022). Taken together, these findings may suggest that larger mouth-hooked sharks may have to expend less energy per unit time during the fight and are thus less stressed and recover more quickly than their smaller counterparts. This difference in exertion during the capture process between different sized sharks requires further research. For the species studied to date, it seems that sharks are more resilient to capture if hook placement is in the mouth, and that reducing fight times may not necessarily increase PRS for these animals. However, given that reduced fight times remain important in improving PRS for tail hooked sharks, reducing fight times may still be a useful step in best practice guidelines, unless the placement of the hook is known during the fight (which is challenging).

3.3.3. *Handling*

Sharks subject to C&R are usually much larger than the teleost fish on which research to date has focused; as a result, the handling techniques used for these animals are markedly different and, given the difficulty of boarding large specimens may result in higher stress levels and more severe physical injury. Initially, whether in-water or on a vessel, the handling period represents a period of hypoxia whilst sharks are held motionless in order to free them from the hook, take measurements and/or photos, or attach tags (Whitney et al., 2017). The level of hypoxia that handled sharks experience likely depends on (1) the ventilatory strategy of the species, (2) water temperature, and (3) whether the shark is handled in the water or on-deck. The physiological response of sharks to hypoxia in the wild is varied and can be species-specific (Speers-Roesch et al., 2012a, 2012b) but is generally characterised by bradycardia (decreased heart rate), accompanied by a decrease in oxygen use and either an increase in swimming speed (for ram ventilators) or a decrease in activity (for species capable of buccal pumping e.g. lemon shark; Brill and Lai, 2015). Where these mechanisms fail to compensate for a lack of oxygen (e.g. during prolonged handling), necrotic and apoptotic mechanisms may increase (Lipton, 1999), leading to a decline in brain electrical activity, which in turn arrests respiratory drive (Nilsson and

Östlund-Nilsson, 2008). In general, fish replace their pool of adenosine triphosphate in cerebral tissue once per minute (Nilsson & Nilsson 2008), meaning that unless replenished, fish can risk lethal brain damage after just one minute, even if they have a low metabolic rate. The tolerance of fish to hypoxia does not vary with fish body size (Nilsson & Nilsson, 2008), but instead varies depending on individual species ecology, with large endothermic species that have high O_2 stores likely to fare better, e.g. shortfin mako shark (Sepulveda et al., 2007; French et al., 2015). From the 12 studies reviewed here, sharks that died were not handled for longer (Kruskal Wallis, $n = 148$, $\chi^2 = 0.001$, $p = 0.99$; Fig. 7) than sharks that survived. However, two studies stated a relationship between handling time and PRS (Mohan et al., 2020; Knotek et al., 2022a). For blacktip sharks, longer handling times increased the probability of swimming impairment post-release (Knotek et al., 2022a), which increased the likelihood of depredation. It did not, however, result in direct mortality. This result is documented in other studies showing that handling results in sub-lethal behavioural impairment post-release (Hoolihan et al., 2011; Whitney et al., 2016b; Raoult et al., 2019; Bowlby et al., 2021).

Due to their typically large mass (in comparison to teleosts popular with recreational fishermen), it can often be necessary when angling sharks to subdue them on-board a vessel or beach prior to release. Handling sharks out of the water, or "boarding", can cause damage to gill filaments and expose fish to extreme temperatures (Cook et al., 2015). The additional physical damage, and resulting impact on PRM, derived from boarding is likely more pronounced in shark C&R than in most teleost fisheries. Given the large mass of commonly angled shark species, boarding and handling often require forceful and/or damaging practices (such as the use of snares for boarding or forceful restriction of the animal once onboard) that may lead to physical injuries not seen in teleost C&R angling. Furthermore, the lack of lateral and ventral skeletal structures in sharks may make them more susceptible to internal injury and trauma than teleost species may be. The effect of boarding, or beaching, sharks on PRS was directly investigated in four studies ($n = 146$ sharks), but no clear statistical relationship was found. Data were only available for individual sharks from three of these studies (French et al., 2015; Mohan et al., 2020) and only one compared in-water and on-deck handling, making any deeper investigation here tenuous. Within the same species, the effect of handling time on PRS seems to be varied. For blacktip sharks caught off Florida and in the Gulf of Mexico, the anglers, time of year, fight time, water temperature and tagging location were broadly comparable with Whitney et al. (2017), Weber et al. (2020) and Mohan et al. (2020). However, Weber et al. (2020) and Whitney et al. (2017) did not document sharks being removed from the water, and Mohan et al. (2020) reported that all sharks were boarded. Mohan et al. (2020) deduce that a combination of protracted fight and handling times resulted in increased likelihood of mortality, yet this relationship was not found in the other studies. Given the comparable settings, it is possible that boarding sharks, with likely associated trauma and air exposure, may have contributed more to mortality than fight time in this instance. Despite not stating a clear evidence of effect, French et al. (2015) noted that two of the three sharks that died in the study were in-boarded. Given the potential for negative impact of boarding sharks, this is an area that requires further investigation.

3.3.4. Revival

Given the prevalence of ram ventilation among commonly angled shark species, assisted ventilation prior to release (i.e. revival) is likely to play a bigger role in determining PRS than in buccal pumping species (most teleosts and some sharks). For ram ventilators, re-oxygenation requires active swimming and behavioural modifications to initiate and maximise water flow over the gills. To recover oxygen supplies post-release, pelagic sharks are thought to reduce diving (Hoolihan et al., 2011) and increase horizontal movement (Whitney et al., 2016a). This response will be depressed if neurological impairment (either due to hypoxia or acidosis caused by metabolic end products or CO_2) results in the loss of equilibrium, righting reflex, swimming or ventilatory movements (Brill and Lai, 2015). Assisted revival, whereby the shark is towed alongside the boat or pointed into the current to increase gill irrigation and O_2 supply (as described in French et al., 2015) can aid angled sharks by reversing fatigue and motor incapacitation. In teleost species, assisted revival has been shown to reduce swimming impairment post-release (Raby et al., 2015) and reduce the time taken to resume normal behaviour (Raby et al., 2018). Most studies analysed here ($n = 6$) did not state whether sharks were revived prior to release (Gurshin and Szedlmayer, 2004; Heberer et al., 2010,2010b,2010c; Kneebone et al., 2013,2013b,2013c; Danylchuk et al., 2014,2014b,2014c; Kilfoil et al., 2017; Anderson et al., 2021) and others recorded several variants of revival prior to release. No study considered it specifically with regards to PRS. Participating anglers and skippers in Knotek et al. (2022) and Whitney et al. (2017) revived sharks on a case-by-case basis, with the authors scoring sharks' release condition using a modified scale proposed by (Hueter et al., 2006). In both studies it was reported that sharks that took less time to be revived were more likely to survive, however, this approach does not allow for an assessment of the benefit of revival and rather only characterises the sharks condition prior to release. Only four of 81 sharks released in Weber et al. (2020) were revived and this factor was not discussed in relation to PRS. French et al. (2015) revived all sharks as standard practice, unless they had to be boarded for tagging or line disentanglement ($n = 7$, 21%) and noted that boarded sharks were less likely to survive. In this case the effects of boarding and a lack of revival may have acted in concert to decrease PRS for those animals, making individual effects challenging to disentangle. The benefit of assisted revival is still, therefore, largely unknown, and future research should seek to address how best fishers can aid in the recovery of sharks prior to release.

3.5. The role of water temperature

Capture has been shown to cause sharks to heat up (Harding et al., 2022) and higher water temperatures (proportional to species-specific geographic ranges, e.g. Fig. 2) can cause fish to fatigue faster when swimming (Blasco et al., 2020). For both endo- and ectothermic species, this is due to a combination of (1) increased basal metabolism (i.e. oxygen demand, Lear et al., 2017), (2) decreased availability of dissolved oxygen in the water, and (3) decrease in blood-oxygen affinity at higher temperatures (Barcroft and King, 1909). Together these processes reduce aerobic scope faster at higher temperatures, likely leading to an increase in stress hormone expression (Manire et al., 2001) and, ultimately, physiological collapse (Schulte, 2015). The effect of water temperature on PRS is likely to be more pronounced for sharks than for teleosts due to the proportionally greater increase of metabolic rate for sharks at higher water temperatures (Watanabe and Payne, 2023). Within the group, endothermic sharks, such as lamnids, are much less affected by increased temperatures than ectothermic sharks due to possessing haemoglobin with an increased affinity for O_2 at higher water temperatures (Morrison et al., 2015; Bernal et al., 2018). No study linked PRS with water temperature for endothermic sharks, but there are instances where water temperature has been linked to PRS for ectothermic sharks. For example, high mortality rates were observed in neonatal blacktip reef sharks (*Carcharhinus melanopterus*) in experimental conditions following exhaustive exercise in water temperatures of 33 °C (the upper thermal limit for the species, Bouyoucos et al., 2020). Sea water temperatures at the time of capture close to the upper end of species' thermal limits were found to negatively affect PRS in two studies, on lemon and blacktip sharks (Danylchuk et al., 2014,2014b, 2014c; Weber et al., 2020), and resulted in longer post-recovery times for blacknose sharks (*Carcharinus acronotus;* Knotek et al., 2022a). Danylchuk et al. 2014,2014b,2014c suggest that water temperature explains the most variance in PRS for lemon sharks, with higher rates of mortality at greater temperatures, and Weber et al. (2020) indicate that a model including both temperature and release condition predicted post-release mortality for shore-caught sharks. Whitney et al. (2017) show that for blacktip sharks, two of three mortalities occurred at the highest temperatures recorded in the study, although this was not statistically related to PRS. While these studies suggest water temperature could play a crucial role in determining the survival of released sharks, none of the best practice guidelines analysed encourage anglers to avoid fishing in particularly warm waters or during the hottest periods of the year. This could be due to the perception that there would be a limited appetite in the angling community to avoid fishing in waters at species-specific temperature extremes due to negative effects on PRS. An additional consideration in warmer regions where boarding sharks is common, for instance the Gulf of Mexico (Whitney et al., 2017; Mohan et al., 2020), is the effect of air temperature on PRS. In such a circumstance, Mohan et al. (2020) deduce that limiting air exposure may increase PRS. For both water and air exposure, more research is needed to clarify the extent to which temperature affects PRS in different species. Precautionary suggestions to restrict fishing activities to waters within the core range of targeted species could be included in angling guidelines, especially in warm seas.

3.6. Sex

The capture likelihood of sharks can be sex specific, often with one sex more likely to be captured than the other (Kanive et al., 2015) due to the spatial segregation by sex of pelagic sharks (Mucientes et al., 2009; Kock et al., 2013; Braccini and Taylor, 2016; Maxwell et al., 2019). As well as susceptibility to capture, there may also be sex-specific differences in response to capture. For instance, capture-induced parturition has been shown to be widespread for elasmobranchs discarded in commercial fisheries (Adams et al., 2018), which, in turn has been shown to affect offspring fitness (Finotto et al., 2021). Whilst all studies reviewed recorded sex of individual sharks as part of sampling activities, only Knotek et al. (2022) considered it in relation to PRS and found no difference between sexes. Tabulated sex data with survival outcomes were available for 160 individual sharks from seven studies (58%; n = 105 females, and n = 55 males; Fig. 8). Of these sharks, significantly more males survived (92%, n = 51) than females (76%, n = 80; two proportion z-test with Yates' continuity correction, $\chi^2 = 7.6$, p = 0.02). However, these data may be skewed: (1) by the sample of common thresher sharks released with trailing gear detailed by Sepulveda et al. (2015) which suffered low PRS (22%, n = 9) but were almost exclusively female sharks (89%, n = 8); and, (2) by the sample of blacktip sharks released in the eastern Gulf of Mexico detailed by Mohan et al. (2020), which were exclusively female sharks (n = 7) with 71% (n = 5) being predated upon release. Irrespective of these potential caveats, the attention paid to sex-specific differences in PRS could be improved. An obvious area for future research could be addressing knowledge shortfalls on the effect of C&R angling during gestation.

3.7. Global Best Practices for Catch-and-Release Angling

Web searches using Google yielded 13 C&R best practice guidelines that made specific reference to sharks (Fig. 9). Of the 17 individual best practices identified by Gallagher et al. (2017), the six most frequently occurring in these 13 best practice guidelines were, in the order of a typical angling event: preparing release gear prior to angling (70%; n = 9 guidelines), using circle hooks (70%; n = 9 guidelines), refraining from boarding sharks (92%; n = 12 guidelines), resuscitating (reviving) sharks prior to release (77%; n = 10 guidelines), releasing sharks by removing the hook (100%; n = 13 guidelines) or releasing sharks by cutting the line (85%; n = 11 guidelines). No guidelines recommended avoiding silty water or cutting sensitive shark species free at capture, both also recommended by Gallagher et al. (2017). There is misalignment between the suggestions given by these guidelines and the focus of scientific research to date. While both research and guidelines give high importance to the use of circle hooks and minimisation of handling time, the high interest in fight time and environmental conditions in research is not reflected in any of the guidelines. Furthermore, potentially critical aspects of the fishing practice such as revival, which is commonly mentioned in guidelines, have so far been overlooked in scientific studies, probably due to being infrequent in practice.

Catch and release guidelines for shark angling often involved practices that lacked underpinning field-specific research, and are instead perceived benefits. Of the 13 guidelines examined, only 38% (n = 5) specifically mention recreational angling research programmes (the remaining eight did not state whether they were scientifically based). While it could be beneficial to retain these long lists of recommended actions until more definitive proof of effectiveness for PRS reduction is found, in some cases it can be useful to have a shorter set of guidelines

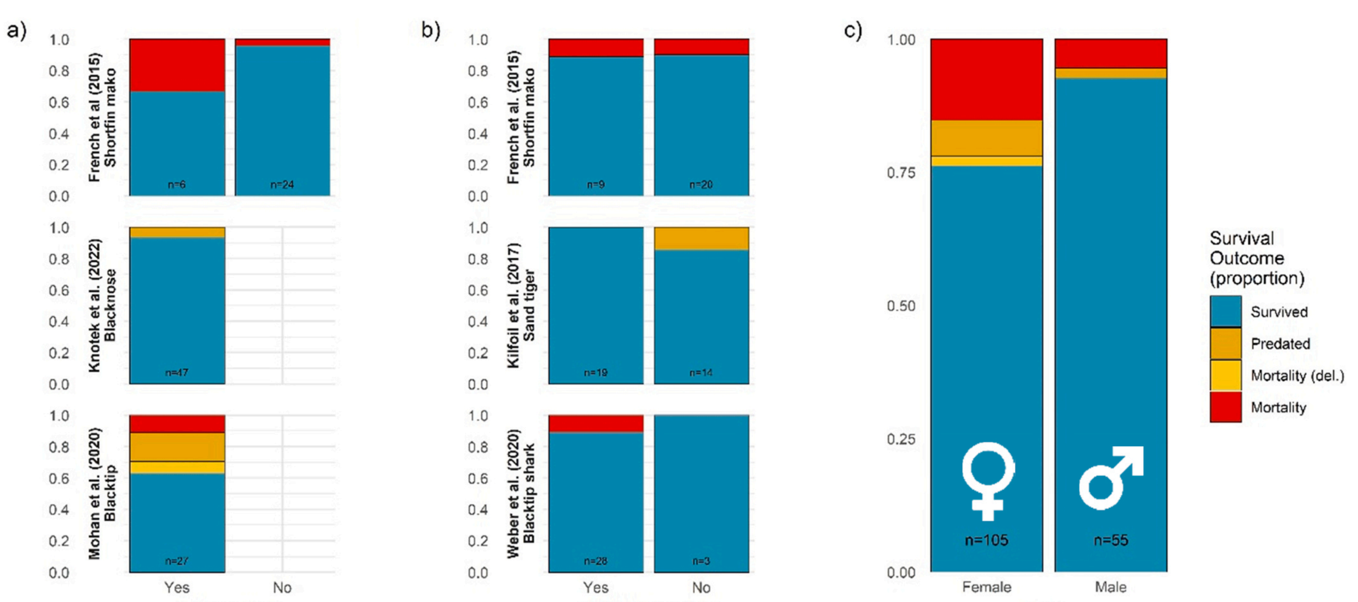

Fig. 8. Meta-analysis of post-release survivorship in relation to in-boarding, hook removal and sex. Sample size for each group is given at the bottom of the respective bar. "Mortality (del.)" refers to delayed mortality.

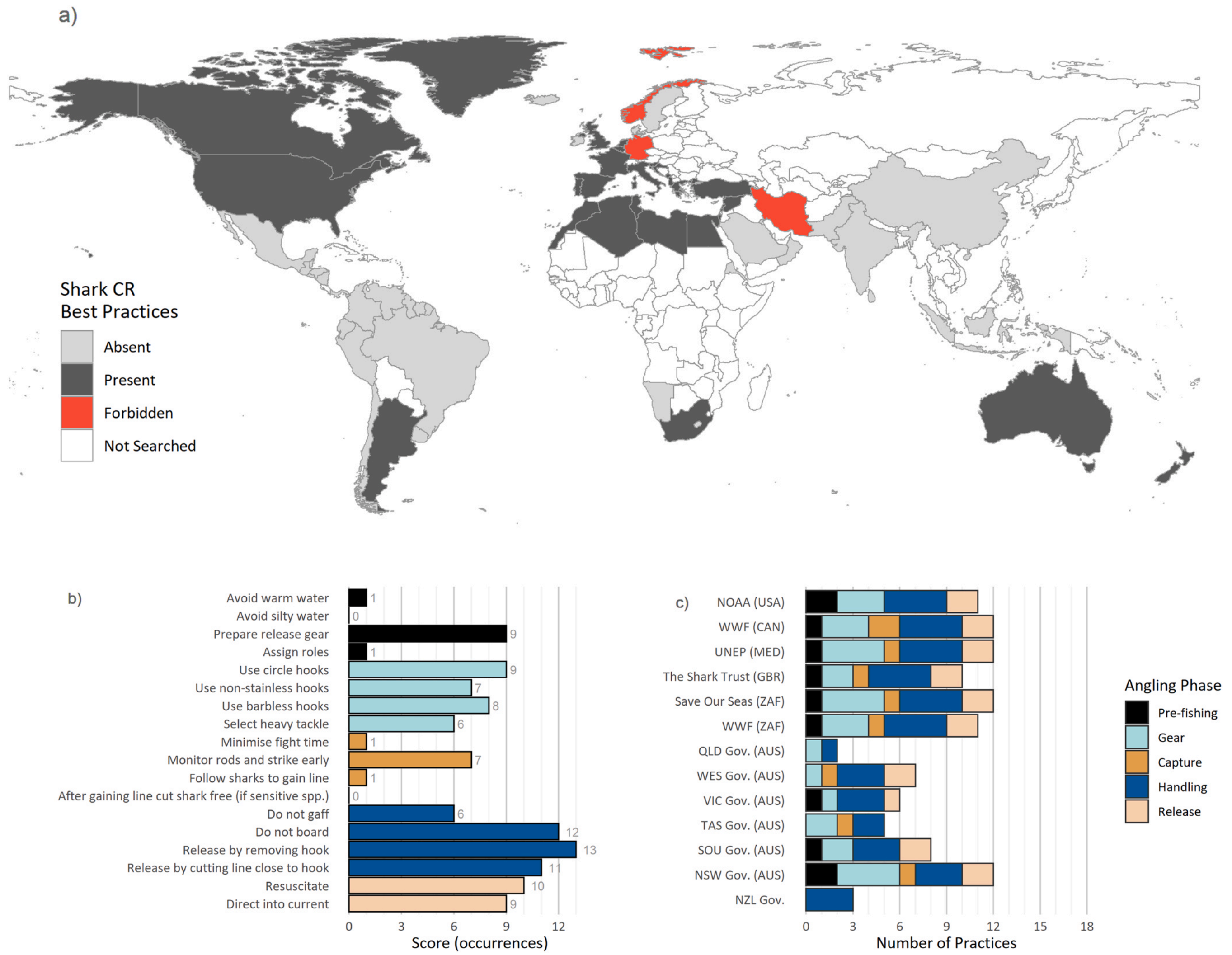

Fig. 9. Summary of global shark catch-and-release guidelines. a) Map detailing the presence and absence of shark catch-and-release angling best practices from Google searches. b) bar plot showing the prevalence of individual practices (*as per* Table 2) for all available guidelines documents pooled, and, c) stacked bar plot of practices in "b" by organisation, country and angling phase.

Box 2
Candidate best practices.

(1) Non-stainless circle hooks should be used wherever possible, which can promote mouth-hooking, and would also rust out (see "2") if left in the animal.
(2) If hook removal requires additional handling or air exposure, the line can be cut close to the hook to release the shark.
(3) Sharks should be left in the water, wherever possible, and towed for a short period to increase gill ventilation prior to release.
(4) Species-specific temperature extremes should be avoided

that are easily remembered by anglers. The candidate best practices in Box 2 are suggested based on our review, stated with the caveat that C&R research for sharks is currently lagging that of other sportfish (e.g. bass, salmonids and bonefish), thus would require further research allowing a more robust meta-analysis. Other steps may also be applicable on a species-specific basis, which would be informed by specific biology.

4. Conclusions: future research and overcoming the issue of sample size

Recreational angling for sharks occurs globally and exposes many more shark species than data exist for to the capture and release process (Gallagher et al., 2017a; Kilfoil et al., 2017). Despite this, research on PRS of sharks in recreational fisheries is limited to three countries and eight species (Gurshin and Szedlmayer, 2004; Heberer et al., 2010, 2010b,2010c; Kneebone et al., 2013,2013b,2013c; Danylchuk et al., 2014,2014b,2014c; French et al., 2015; Sepulveda et al., 2015; Kilfoil et al., 2017; Whitney et al., 2017; Mohan et al., 2020; Nick Weber et al., 2020b; Anderson et al., 2021; Knotek et al., 2022a). Given the need for species-specific best practices to be developed (Cooke and Suski, 2005) and the broad distribution and temperature niches of sharks, the most obvious areas for future research are to expand the knowledge base in terms of the number of species studied and the number of locations that species are studied over. Small sample sizes often precluded robust analyses in the studies analysed here. At present, gaining a detailed understanding of survival outcome post-release can only truly be achieved with biologging tags, which have a high per-unit cost (i.e. hundreds to thousands of US dollars per tag). Consequently, most studies' sample sizes are limited by budget availability. One way to circumvent this would be to develop a collaborative online database for PRS estimates derived from electronic tracking data, whereby individual shark data would be available to researchers. Metadata on the angling process were only available for 53% of individual sharks studied (208 of 396 studied), but if all these data were available (for all individual sharks and recorded variables), then future reviews could make more robust conclusions. To further increase sample sizes, data could be gleaned from other studies where survivorship was not the key aim, yet scientists adopted recreational methods for spatial ecology studies using biologging tags. In such instances, the fate of tagged individuals in the short term could provide additional clues in terms of responses to capture. A preliminary investigation of a subset of such papers found inferences on the fate of tagged individuals but with information lacking on the angling event, and so they could not be considered.

The research summarised here comprises scientific peer-reviewed activities, yet inter-study comparisons were challenging. This was, in part, due to differences in recording of the angling process. To enable greater statistical power, together with increased sample sizes, future studies could consider the standardised angling stages we consider here. In particular, the unhooking and revival processes, and environmental conditions of captures and release (e.g. temperature, salinity and turbidity).

There is a significant and relevant human aspect in the management of recreational fisheries, which is beyond the scope of this review. Research has shown that C&R is widely practiced in marine recreational fisheries (Ferter et al., 2013) and that anglers perceptions can marry well with research findings (French et al., 2019). To aid in developing C&R guidelines and maximise their uptake, a next stage beyond identifying beneficial fishing actions would be to collaborate with the recreational fishing community to refine and implement evidence-backed C&R guidelines.

As the interest in recreational shark fishing grows (Mcclellan Press et al., 2016) meta-analyses of specific C&R research should form the basis of evidence-backed best practice guidelines. Here, we have outlined the current state of shark C&R science and the current perception of how anglers should treat sharks through published best practice guidelines. PRS for sharks in the studies reviewed is generally high for most species, but, despite rigorous research (Table 3), the science does not yet provide a firm footing for most best practices in isolation, suggesting a precautionary approach is best. Future research on this topic should aim to (1) increase sample sizes through global collaboration, and (2) harmonise scientific design to increase comparability across regions and species. With further angler and scientific collaboration, the sustainability of C&R shark fishing could increase further through adaptive management of the activity based on flow of information between managers, scientists and stakeholders.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Witt, Horton and Hawkes report that financial support was provided by the European Maritime and Fisheries Fund.

Data Availability

Data is available from published research or open-source internet pages.

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